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Brief Communication

Comparing rates of molecular and morphological evolution identifies multiple speciation trajectories in a diverse radiation of skinks

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Abstract

There is increasing recognition that the process of species divergence is not uniform across the tree of life, and that newly diverged taxa may differ in their levels of phenotypic and genetic divergence. We investigate the relationship between phenotypic and genetic differentiation across the speciation continuum using sister pairs from a large ecologically diverse radiation of Australian skinks, the Tribe Eugongylini, a high-quality alignment of genomic sequence data, and morphometric data for 90 lineages across the radiation. Based on the framework proposed by Struck et al. (2018) for comparative study of species divergence, we used latent class regression to test for multiple speciation "trajectories." We found evidence for multiple relationships between genetic divergence and morphological disparity for recently diverged sister taxa, which we summarize into 2 broad patterns. One of these patterns is characterized by relatively rapid morphological differentiation for pairs with greater disparity in environmental variables, consistent with expectations of ecological speciation. The second pattern shows accumulation of both morphological and genetic differences in proportion to each other, consistent with gradual speciation. Our study shows how heterogeneity in speciation processes can be captured in a comparative framework.

Keywords: ecological speciation, cryptic speciation, morphological evolution, genetic divergence, sister pairs

Introduction

The relationship between morphological variation, ecological divergence, and evolutionary independence during the process of speciation has been the subject of much debate. Taxonomists typically use morphological differentiation as a proxy for reproductive isolation between lineages; however, there is increasing recognition that many morphologically indistinguishable lineages are also strongly reproductively isolated (Bickford et al., 2007; Singhal et al., 2018). "Cryptic species" identified primarily from genetic data appear to be surprisingly common in nature (Chenuil et al., 2019; Fiser et al., 2018). Although ecological speciation, driven by adaptive divergence to different niches, has been widely observed and has strong theoretical support (Shafer & Wolf, 2013; Sobel et al., 2010), the existence of cryptic species suggests that species can arise in the absence of divergent adaptation (Rundell & Price, 2009; Struck & Cerca, 2019).

Theoretical models have shown that mutations which are selectively neutral, beneficial, or slightly deleterious can become fixed in allopatric populations, which can result in low fitness when combined in a hybrid (Nosil & Flaxman, 2011). Such incompatibilities may involve few genes with large phenotypic effects or many genes with small effects, and the probability of incompatible substitutions arising in diverging lineages can increase exponentially with divergence time (Dagilis et al., 2019; Orr & Turelli, 2001). Reduced fitness in hybrids may be due to an intermediate phenotype which is unfit in either parent environment (extrinsic incompatibility) or disruptions to key metabolic or developmental processes (intrinsic incompatibility) (Seehausen et al., 2014; Sobel et al., 2010). Leaving aside the possibility of rapid chromosomal speciation (Bogdanov et al., 2023; Potter et al., 2017; Sobel et al., 2010), cryptic species may arise when two geographically isolated lineages accumulate many small-effect genomic incompatibilities over a long period of time leading to intrinsic incompatibility on secondary contact (Coughlan & Matute, 2020; Mikkelsen & Irwin, 2021). Ecological speciation might proceed more rapidly due to selection on a small number of large-effect genes resulting in extrinsic incompatibility, with intrinsic incompatibilities arising later once the two lineages have been evolving independently for some time (Matsubayashi & Yamaguchi, 2022; Nosil et al., 2009; Seehausen et al., 2014).

A key prediction of this view of divergence mechanisms is that the process of speciation is likely to proceed at different rates depending on the eco-evolutionary context of the lineages in question (Scopece et al., 2007; Shin & Allmon, 2023). Struck et al. (2018) formalized this notion in a framework for understanding and investigating speciation trajectories. They predict that while most species pairs will accumulate

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phenotypic differences in proportion to time since divergence, some pairs will have proportionally very high morphological disparity (e.g., in adaptive radiation), while others will have very low morphological disparity relative to divergence time, as expected in cases of morphological stasis. These three broad patterns represent what we refer to as "gradual" speciation, ecological speciation, and cryptic speciation, respectively (Figure 1). These different processes may lead to heterogeneity in the relationship between morphological disparity and genetic divergence within and between taxonomic groups (Wollenberg Valero et al., 2019). This heterogeneity highlights the need to consider genomic, morphological, and ecological divergence axes in the characterization of biodiversity (Bolnick et al., 2023; Johannesson et al., 2024).

We apply this model to our study system, a diverse radiation of Australian lizards, to assess the patterns of divergence in closely related lineages. Lizards have been recognized as excellent systems for the study of speciation due to their high eco-morphological diversity, easily measured adaptations (which often involve morphometric changes), and low dispersal capacity which results in strong phylogeographic structuring (Camargo et al., 2010; Losos, 2009; Nunes et al., 2022; Wollenberg Valero et al., 2019). We utilized recently published data on the Australian radiation of skinks, the Tribe Eugongylini (Shea, 2021), including a lineage-level coalescent phylogeny (Bragg et al., 2024; Ivan et al., 2021). This tribe is known to contain instances of both cryptic speciation (Afonso Silva et al., 2017; Singhal et al., 2018) and adaptive evolution through morphological convergence (Blom et al., 2016; Dolman & Stuart-Fox, 2010). This radiation, dated to the early Miocene (Oliver & Hugall, 2017), includes approximately 125 taxonomically recognized species across 18 genera, and an additional 75 taxonomically unrecognized intraspecific lineages have been identified from phylogeographic evidence (Bragg et al., 2024). The Tribe includes species inhabiting a wide range of habitats across the Australian continent, from the Tasmanian snow skinks (*Carinascincus*), to the rainbow skinks of the wet tropics (*Carlia*), and the snake-eyed skinks which specialize on rocky crevices and arboreal substrates in the arid zone (*Cryptoblepharus*) (Blom et al., 2016; Wilson & Swan, 2017). Many genera have recently undergone rigorous taxonomic revisions (e.g., Horner, 2007) and the rate of new species being recognized and described has plateaued following a rapid increase in the past decades (Flanagan et al., 2024), giving confidence that any taxonomically unrecognized lineages are likely to be truly morphologically undiagnosable (Chenuil et al., 2019; Shin & Allmon, 2023)—meaning that they cannot be distinguished by morphological traits alone (see Supplementary Text S1 for details of this terminology). A combination of well-defined intraspecific lineages and divergences spanning the "gray zone" of speciation—a range of divergence estimates in which species status, judged by reproductive isolation, is inconsistent across taxa (Roux et al., 2016; Singhal & Bi, 2017; Singhal et al., 2018)—mean that taxa can be sampled from across the speciation continuum in this system rather than simply comparing "end products" (i.e., fully reproductively isolated species) (Matsubayashi & Yamaguchi, 2022; Sobel et al., 2010). We used a sister pairs approach to look at the relationship between neutral genetic divergence and morphological disparity across the phylogeny (Freeman et al., 2023; Johannesson et al., 2024; Nunes et al., 2022; Struck et al., 2018). We then used latent class regression to identify groups of species pairs with different ratios between these two variables to test the hypothesis of multiple speciation trajectories. This strategy allows us to avoid assuming that all pairs of taxa must be on the same speciation path, a limitation which has hindered previous comparative studies of speciation (Bolnick et al., 2023; Stankowski & Ravinet, 2021).

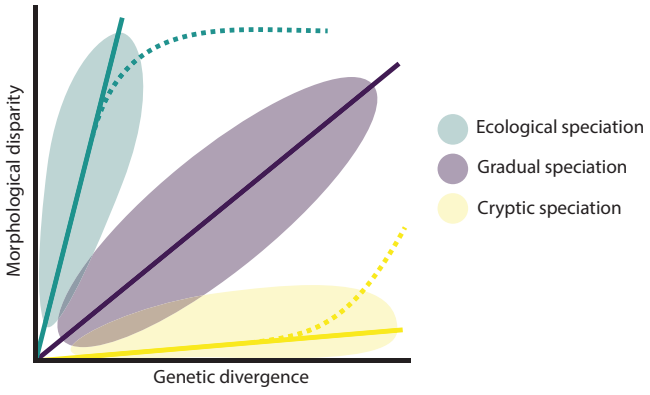

Figure 1. Speciation trajectories. Diverging lineages may show a pattern of high morphological disparity and relatively low genetic divergence (ecological speciation), low morphological disparity with relatively high genetic divergence (cryptic speciation), or may accumulate genetic and morphological changes in proportion to one another (gradual speciation). Cryptic species pairs may accelerate their rate of morphological differentiation on secondary contact due to reinforcement (dashed curve, bottom right). Ecological species pairs may slow down their rate of morphological differentiation once adaptation to a new niche is complete (dashed curve, top left). Figure represents the conceptual framework of Struck et al. (2018).

Methods

Pair selection

Sister-taxon pairs (recognized species or intraspecific lineages) were selected based on the lineage-level maximum clade credibility coalescent phylogeny of the Australian Eugongylini presented in Bragg et al. (2024). First, tips with insufficient data were excluded, and sister pairs were then selected from the remaining tips. Bragg et al. (2024) present exon capture data from the same set of individuals as published in Ivan et al. (2021); we therefore utilized the high-quality alignments of concatenated exons from Ivan et al. (2021) to estimate sequence divergence, with assignments of individuals to lineage level taken from Bragg et al. (2024) (Supplementary Table S1). Any tips without sequences in the alignment of Ivan et al. (2021) were excluded.

All lineages represented in the phylogeny are distinguishable based on morphology, geographic distribution, or both. Across the clade, intraspecific lineages within a single described species are defined by nonoverlapping geographic ranges (see Bragg et al. (2024) for details). In the absence of a large number of genotyped vouchered specimens, we used museum vouchers morphologically identified to species level for our morphometric data set. We created polygons based on extensive published data (Afonso Silva et al., 2017; Bell et al., 2010; Bragg et al., 2024; Chapple et al., 2011a, 2011b; Dissanayake et al., 2022; Dolman & Moritz, 2006; Donnellan et al., 2009; Dubey & Shine, 2010; Haines et al., 2014; Horner, 2007; Horner & Adams, 2007; Moussalli et al., 2009; Potter et al., 2016, 2018, 2019; Rittmeyer, 2014) to define the geographic distributions of intraspecific lineages,

and vouchered museum specimens were then assigned to lineages based on these polygons (Supplementary Figure S1). Vouchers which could not be confidently assigned to a lineage were excluded. Any tips with fewer than five vouchered specimens across the collections of the Australian National Wildlife Collection (ANWC), Australian Museum (AMS), Queensland Museum (QM), and South Australian Museum (SAMA) were excluded.

After filtering, we selected all available pairs of closest relatives for pairwise comparisons for two reasons. First, this ensured that all pairs represented statistically independent comparisons (each tip was only included once and no overlapping phylogenetic paths existed between pairs of taxa) without introducing bias through deliberate selection of particular pairs (Harvey & Purvis, 1991; Lanfear et al., 2010). Secondly, analyzing differences between sister pairs of taxa reduces the impact of the node density effect on estimation of genetic divergence (i.e., underestimation of long branch lengths due to sparse sampling of taxa and/or multiple substitutions at the same site) (Hugall & Lee, 2007; Lanfear et al., 2010). The exception to this rule was for the pair *Carlia munda ETE* and *C. munda broad*: *C. munda ETE* was chosen in preference to the closest relative *C. munda melville* as more vouchered specimens were available for this lineage. In total, 45 pairs were selected for analysis (Figure 2). Pairs were classified as either morphospecies or morphologically undiagnosable based on published taxonomic descriptions (Figure 2; Supplementary Table S2). Morphospecies pairs are taxonomically described species with at least one diagnostic morphological character, while morphologically undiagnosable pairs are undescribed intraspecific lineages or described taxa without diagnostic morphological characters (see Supplementary Text S1 for further details).

Genetic divergence

Neutral genomic divergence was estimated as the number of synonymous substitutions per site between taxa in a pair. We obtained unbiased estimates of branch length between pairs using a triplet approach, where a triplet includes a pair of taxa and an outgroup. Genetic data were taken from the alignment of 1268 filtered and concatenated exons in Ivan et al. (2021). For each pair, we chose the closest relative to the most recent common ancestor of the pair in the phylogeny as an outgroup; where the closest relative was a clade, one tip was randomly chosen from this clade as the outgroup. For each taxon in a triplet, all sequences in the alignment were extracted and used for analysis. The number of individuals per taxon ranged from one to eight with a mode of two (Supplementary Table S1); however, the lineage-level phylogeny of Bragg et al. (2024) has a single tip per lineage. Therefore, we used IQ-Tree2 (Bui et al., 2020) to estimate tree topology between individuals for taxa with multiple individuals, and manually rooted these triplet trees on the outgroup clade. One triplet (*Cryptoblepharus ruber a2* and *Cryptoblepharus megastictus*, with *Cryptoblepharus ruber a1a3* as the outgroup) was excluded from further analysis as the two ingroup taxa did not form reciprocally monophyletic clades of individuals.

The tree topology for individuals for each triplet and the aligned sequences were then used as input for *codeml* in PAML4 (Yang, 2007) to estimate synonymous substitution rate under the branch model. The analysis was constrained to apply a single codon evolution model to all individuals in a taxon. The mean branch length between sister pairs based on the expected number of synonymous substitutions per site was calculated by successive averaging of sister branch lengths from tip to root (Ritchie et al., 2022), and we used this value as the measure of genetic divergence (Supplementary Table S4). There was a strong correlation between genetic divergence calculated from the triplets in PAML4 and branch length in the coalescent phylogeny from Bragg et al. (2024) (Supplementary Figure S2).

Morphological disparity

For each taxon included in the set of pairs, at least five and up to 10 vouchered specimens (Supplementary Table S1) were measured for the following set of morphometric traits: snout-vent length (SVL), forelimb length, hindlimb length, trunk length, head length, head depth, head width, hand length, and foot length. These traits were chosen as they have been shown to be ecologically relevant in skinks and other lizard taxa (Blom et al., 2016; Cordero et al., 2021; Dolman & Stuart-Fox, 2010; Mahler et al., 2010). Although many species differ in color and pattern as well as morphometric traits (e.g., Figure 3B–D), we were unable to include these characters in our analysis as coloration is poorly preserved in museum spirit collections (Sistrom et al., 2013). Forelimb length and hindlimb length were calculated as the sum of two and three linear measurements along the limbs, respectively; all other traits were taken as simple linear measurements. Specimens used in the morphometric data set were not genotyped but were assigned to intraspecific lineages based on geographic distribution (see *Pair selection* and Supplementary Figure S1). Morphological measurements for all individuals can be found in Supplementary Table S3. To correct for body size-dependent increases in variance, we took the natural log of all measurements to use in further calculations.

The Bhattacharyya distance, a generalization of the Mahalanobis distance which allows the standard deviations of each sample to differ (Bhattacharyya, 1946), was used to calculate morphological disparity between the taxa in each pair with the package *fpc* (Hennig, 2020) in R (R Core Team, 2021) (Supplementary Text S2). This definition of morphological disparity allows for morphologically undiagnosable taxa to have high morphological disparity if the means of the multivariate normal distributions are far apart but the distributions overlap. We controlled for potential effects of allometry due to differences in sample age profiles by taking the residuals of a linear regression of morphological disparity against a measure of difference in median age between taxa in a pair (see Supplementary Text S3 for details).

The variance of morphological disparity is expected to increase over the divergence time between sister pairs of taxa. To correct for heteroscedasticity due to time dependence, we used genetic divergence of the pair as an indicator of their depth of divergence and divided the age-corrected estimates of morphological disparity by the square root of the genetic divergence of the pair. This approach is standard in sister pair comparisons (Welch & Waxman, 2008). These estimates of morphological disparity, corrected for the specimen maturity ("age") profile of the specimens and heteroscedasticity, were used in all subsequent analyses.

Quantifying patterns of divergence

Each taxon pair provides us with one independent contrast of genetic divergence and morphological disparity. As a first

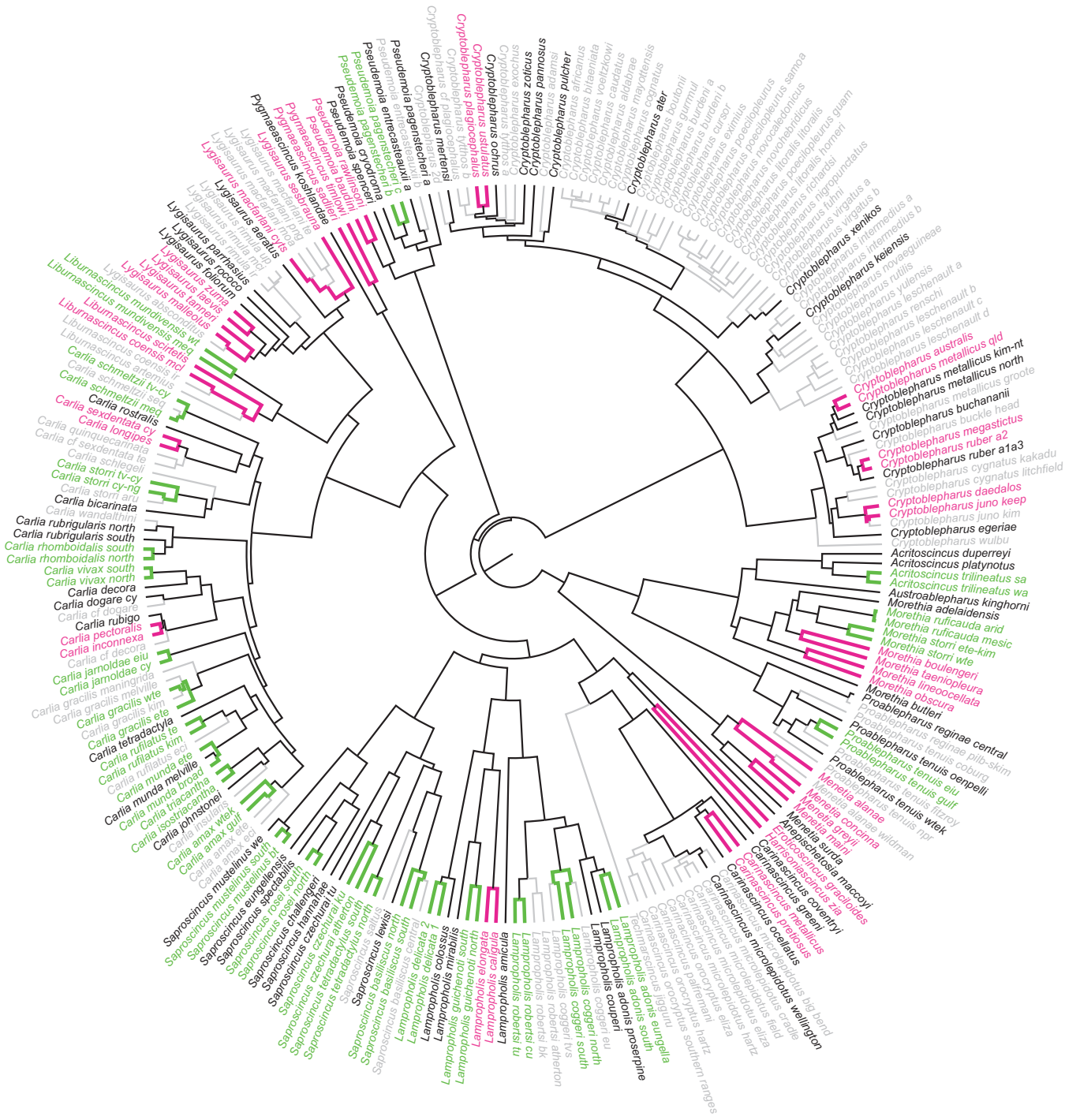

Figure 2. Process of pair selection. Tips that were excluded from the analysis based on limited specimens or sequence availability are shown in gray. From the remaining tips, pairs of closest relatives were selected for inclusion in the analysis—these are highlighted (bold) in green (morphologically undiagnosable pairs) and pink (morphospecies pairs). Black tips show taxa that were retained during pair selection but are not part of a pair. Phylogeny is taken from Bragg et al. (2024).

pass, we used linear regression to test for an overall relationship between genetic divergence and morphological disparity across all contrasts. We also compared the degree of morphological disparity between morphospecies pairs and morphologically undiagnosable pairs using a Wilcoxon rank sum test.

We used the R package *Flexmix* (Gruen & Leisch, 2008) to investigate the relationship between genetic divergence and morphological disparity among pairs. *Flexmix* fits a mixture of linear regression models to the data, in order to test whether there are different clusters of data points supporting different regression models. We used *Flexmix* to fit a mixture of 1–10 linear regression models (i.e., 1–10 clusters) to the contrasts, where each regression model has morphological disparity as response variable and genetic divergence as independent variable. The intercept of each regression model was constrained to the origin, because we expect, on average, no morphological difference between pairs that are not genetically diverged. For each number of regression models, we

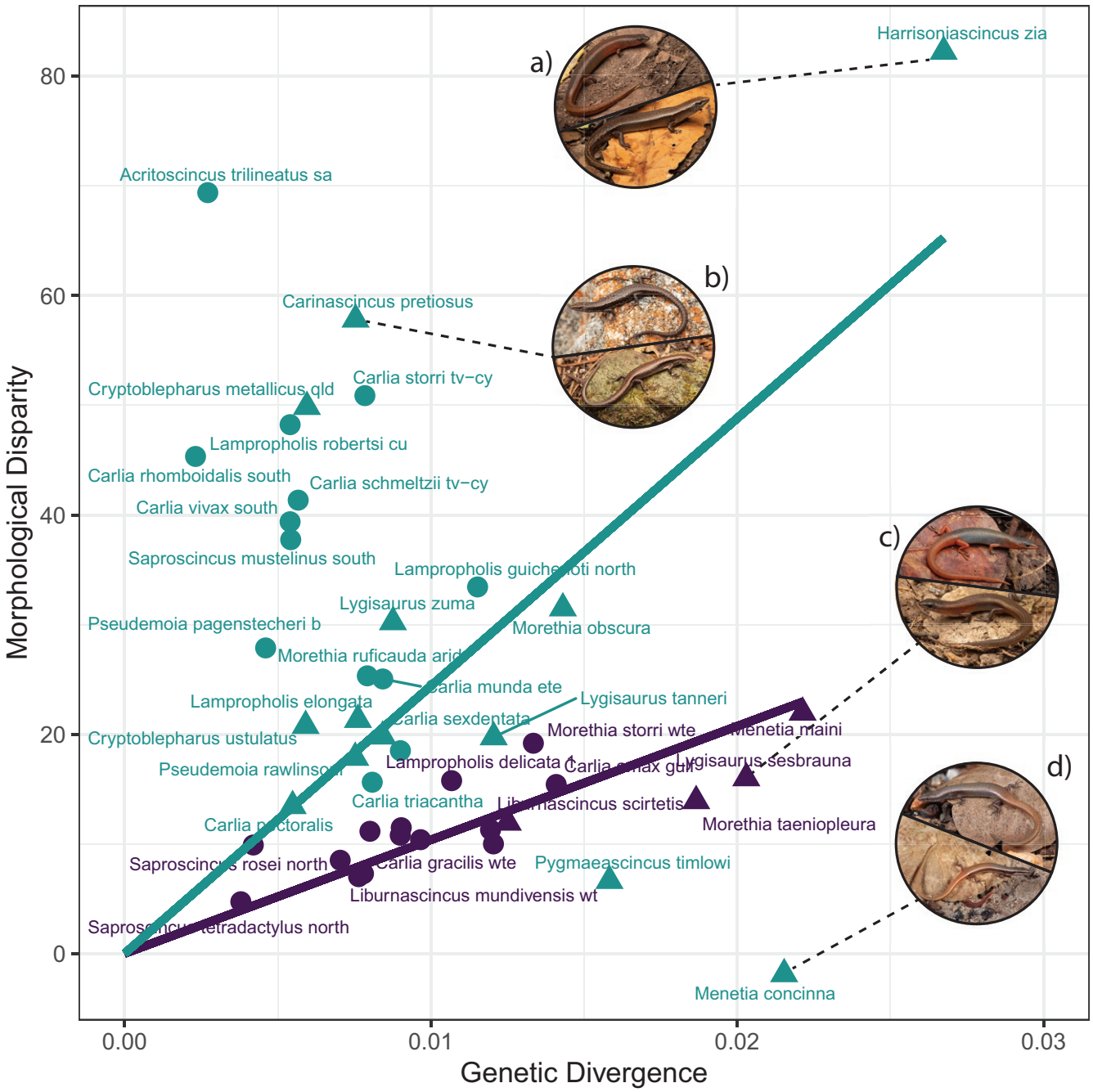

Figure 3. Results of *Flexmix* analysis with two clusters. Points are labeled according to Taxon 1 in the pair as per Supplementary Table S1. Colors show cluster assignment. Morphospecies pairs are shown with triangles and morphologically undiagnosable pairs are shown with circles. Insets show photographic examples of the taxa in four representative pairs: (A) *Carinascincus pretiosus* (top) and *Ca. metallicus* (bottom); (B) *Eroticoscincus graciloides* (top) and *Harrisoniascincus zia* (bottom); (C) *Lygisaurus macfarlani cyts* (top) and *Ly. sesbrauna* (bottom); (D) *Menetia alanae* (top) and *M. concinna* (bottom). Images provided by Wesley Read (A, B, C) and Jordan Mulder (D), and are reproduced in Supplementary Figure S7 at larger size.

ran the EM (Estimate-Maximize) algorithm for a maximum of 1,000 iterations. Model fit was compared using Bayesian information criterion. We replicated the analysis with and without inclusion of the single between-genera pair, and using uncorrected morphological disparity estimates, to gauge sensitivity of the results to these factors (Supplementary Text S4).

Ecological correlates of divergence patterns

The best-fit model from the *Flexmix* analysis includes two distinct clusters of contrasts showing different patterns of divergence (see *Results*). We sought to test what factors may be driving these differences. We hypothesized that pairs with a higher ratio of morphological disparity to genetic divergence may also have higher ecological disparity if morphological divergence is driven by adaptation to different niches.

We used several measures of ecological disparity to test this hypothesis (Supplementary Table S4). We obtained ecological data for each named species from a curated set of species distribution points taken from the Atlas of Living Australia (ALA) via the ALA Spatial Portal (ALA, 2024). For short-range endemic taxa and those with few points in ALA, we supplemented distribution points with genotyped field records

(Bragg et al., 2024). For intraspecific lineages, distribution points were assigned to a lineage if they fell in the distribution polygon of that lineage (see *Pair selection* and Supplementary Figure S1). Any points which could not be assigned to a lineage were excluded. Duplicate records of a single species at a single location were excluded. Ecological variables relating to climate (temperature and precipitation), topography and habitat type were chosen as they have previously been linked to survival and adaptation of lizards in Australia and elsewhere (Llewellyn et al., 2018; McDonald-Spicer, 2020; Tarkhnishvili et al., 2013) (Supplementary Text S5).

For each of the abiotic ecological variables, we calculated the mean for each taxon by averaging across all occurrence records for that taxon and then found the difference of means between taxa in a pair as a measure of disparity for that variable. Additionally, we combined all abiotic variables and used all the points to create a composite measure of abiotic environmental disparity. This measure was calculated as the Bhattacharyya distance (Bhattacharyya, 1946) between taxa under the assumption that variables correlate equally between species within each pair, as described for morphological disparity in Supplementary Text S2. We used vegetation type to measure broad-scale habitat disparity between taxa in each pair. For each taxon, points with unknown vegetation type were excluded, and relative abundance in each vegetation type was calculated by dividing the number of points in each vegetation type by the total number of points for the taxon. Habitat disparity was then calculated as the Bray–Curtis dissimilarity (Bray & Curtis, 1957) between the taxa in the pair. For each of these measures of ecological disparity, we calculated the ratio of ecological disparity to genetic divergence for each pair and used a Wilcoxon rank sum test to test for differences between the clusters identified by the *Flexmix* analysis. Finally, we used a combination of field guide descriptions of recognized species (Cogger, 2014; Wilson & Swan, 2017) and field observations of intraspecific lineages to classify the microhabitat of taxa in each pair as same or different. We tested for differences in microhabitat similarity between the clusters with Fisher's exact test.

Results

Disparity calculations for all pairs are found in Supplementary Table S4. Across all contrasts, morphological disparity was not predicted by genetic divergence ($p = .62$). There was no significant difference in the degree of morphological disparity in morphologically undiagnosable pairs compared to morphospecies pairs ($W = 201$, $p = .50$).

The best-fitting model found by the *Flexmix* analysis had two clusters (Supplementary Table S5), and cluster assignment was unchanged regardless of whether the more divergent, between-genera pair was included in the analysis (Supplementary Figure S3, Supplementary Table S6). The first cluster (shown in purple in Figure 3) included 18 of the 44 pairs and showed a strong relationship between genetic divergence and morphological disparity ($p < .001$, $R^2 = 0.94$). The second cluster (shown in teal in Figure 3) contained the remaining 26 pairs and showed a weaker relationship between the two variables ($p < .001$, $R^2 = 0.53$) and, on average, greater morphological disparity relative to genetic divergence. To avoid confusion, we will refer to these clusters as "teal" and "purple" according to their colors in Figure 3. There was no significant difference in the number of morphologically undiagnosable pairs between the two clusters (Fisher's exact test, $p = .11$), and the two clusters are distributed evenly across the phylogeny (Supplementary Figure S6). Results were qualitatively similar when the analysis was run using uncorrected morphological disparity estimates (Supplementary Text S4).

The teal cluster contains two pairs with extremely low levels of morphological disparity relative to genetic divergence: *Pygmaeascincus timlowi–Py. sadlieri* and *Menetia concinna–M. alanae*. These pairs are included in the teal cluster despite not conforming to the same pattern as other teal cluster pairs as the residual variance in the purple cluster is very small, meaning that model fit is maximized when they are included in the teal cluster with high residual variance. We consider these pairs to be outliers as they do not conform to either of the broad evolutionary trends identified in this clade. *Pygmaeascincus timlowi–Py. sadlieri* has low posterior probability for the teal cluster (PP = 0.66), and several other pairs which are intermediate between the two clusters also have low posterior probability for cluster assignment (e.g., *Carlia pectoralis–C. inconnexa*, *C. triacantha–C. isostriacantha*, *Lygisaurus tanneri–Ly. malleolus*, *Morethia storri wte–Mo. storri ete-kim*, and *Saproscincus rosei north–S. rosei south*; Supplementary Table S7).

We found that the teal cluster, which shows higher morphological disparity relative to genetic divergence, also showed significantly greater ecological disparity between sister taxa for several variables compared to the purple cluster (Figure 4). Relative to genetic divergence, composite abiotic disparity ($W = 131$, $p = .01$), elevation ($W = 141$, $p = .03$), and topographic slope ($W = 143$, $p = .03$) had significantly greater disparity for pairs in the teal cluster than the purple cluster. While vegetation, precipitation seasonality, and temperature seasonality also showed higher mean disparity, these differences were not significant. Likewise, although pairs in the teal cluster were more likely to have different microhabitats than those in the purple cluster, this difference was not significant. Disparity in annual mean temperature and precipitation did not differ between clusters.

Discussion

Struck et al. (2018) proposed a conceptual framework that uses the relationship between genetic divergence and morphological disparity to identify cryptic species. Here we extend their framework to categorize three broad type of relationships between genetic divergence and morphological disparity, corresponding to three different modes of speciation. These three categories are an oversimplification, but they are a useful lens through which to interpret the results of our analysis. Our results show a lack of a simple predictable relationship between morphological disparity and genetic divergence across the Australian Eugongylini, which allows us to reject the hypothesis that all pairs of taxa are evolving along a similar trajectory. Similar results showing unpredictable or inconsistent relationships between eco-morphological and genetic divergence across pairs of taxa have been reported in some recent studies (e.g., birds (Freeman et al., 2023); snails (Johannesson et al., 2024)). Instead, the best-fitting model shows two clusters of pairs within the data set, indicating that there are likely to be multiple speciation trajectories in this group. The mean ratio of morphological disparity relative to genetic divergence is higher in the teal cluster than the purple

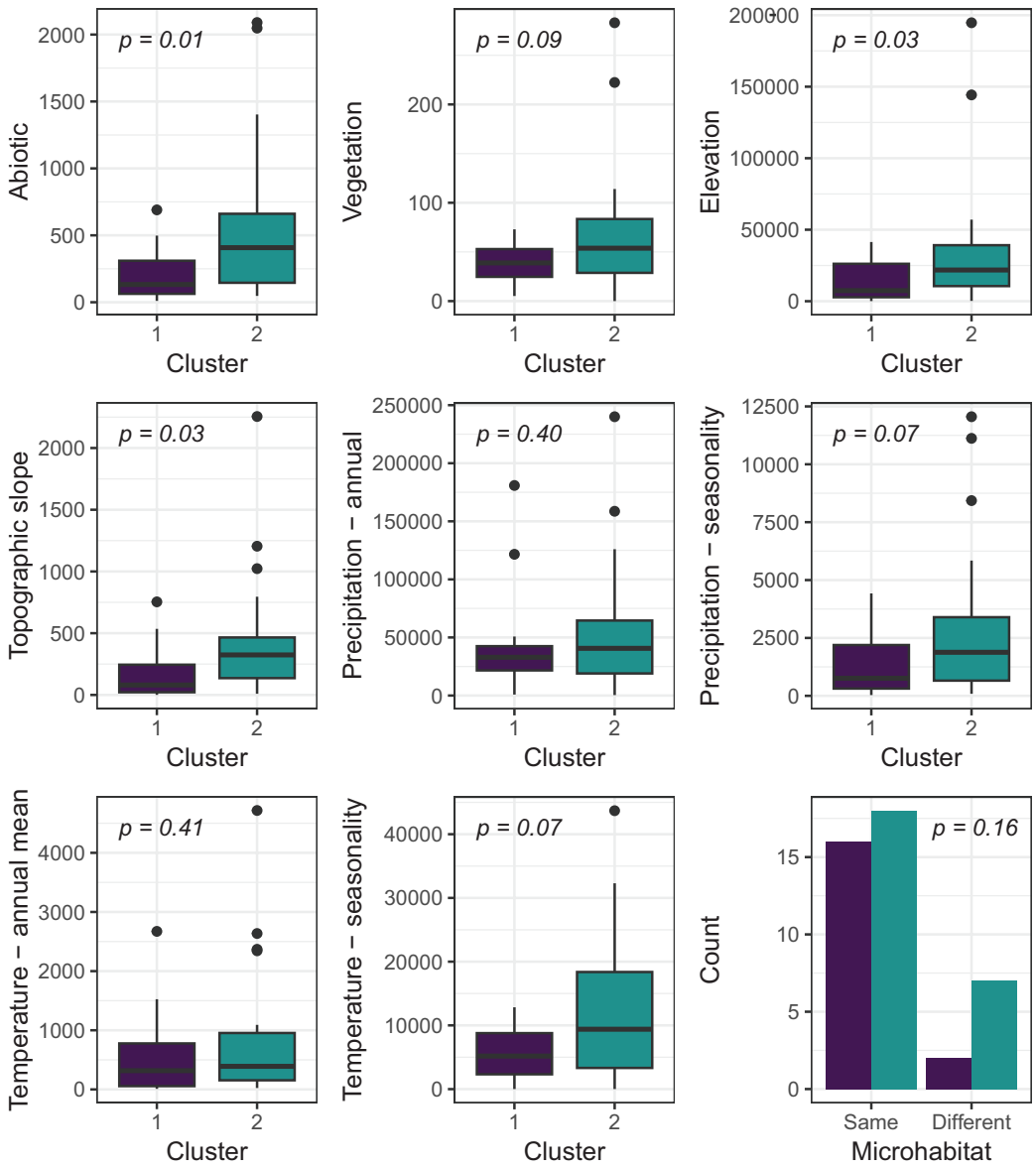

Figure 4. Contrasts in ecological variables for pairs in the two clusters. The y-axis of each panel (except Microhabitat—bottom right) shows the ratio of ecological disparity to genetic divergence. Cluster 1 (purple, left) contains 18 pairs and cluster 2 (teal, right) contains 26 pairs.

cluster, and the former simultaneously shows strong abiotic environmental disparity. The low posterior probability of cluster assignment for some intermediate pairs also suggests that the divergence trajectories exist on a continuous spectrum and are not discrete processes. Our results are consistent with a growing body of literature arguing the importance of considering multiple axes of divergence and accounting for variation between lineages when characterizing speciation patterns at the clade level (Bolnick et al., 2023; Freeman et al., 2023; Johannesson et al., 2024; Kiebacher & Szövényi, 2024; Korshunova et al., 2019; Matsubayashi & Yamaguchi, 2022; Stankowski & Ravinet, 2021).

Ecological speciation, as defined here, occurs when interspecific-level morphological disparity is seen at intraspecific levels of genetic divergence (Struck et al., 2018). Aside from the two pairs with extremely slow rates of morphological evolution (*Pygmaeascincus timlowi–Py. sadlieri* and *Menetia concinna–M. alanae*; Figure 3D) all pairs in the teal cluster have genetic divergence estimates equal to or less than the maximum level of genetic divergence shown by intraspecific lineage pairs (0.014 synonymous substitutions per site). Several of these pairs, such as *Acritoscincus trilineatus sa–A. trilineatus wa*, also have morphological disparity estimates which are comparable to the between-genera pair *Harrisoniascincus zia–Eroticoscincus graciloides* (Figure 3B). The teal cluster therefore conforms to expectations of ecological speciation. This is further supported by the fact that pairs in the teal cluster generally have greater ecological disparity relative to genetic divergence, which is consistent with divergent adaptation to different environments, although the functional link between the morphological and ecological variables measured here is not known. Two of these three significantly higher ecological disparity variables are related to topography (elevation and slope), raising the intriguing possibility that rapid speciation in the Tribe Eugongylini may be driven by elevation gradients. Isolation-by-ecology along

elevational gradients as a driver of speciation has been supported in some other taxa (e.g., insects (Polato et al., 2018); plants (Steinbauer et al., 2016)) and would be consistent with the high levels of endemism seen in topographically complex regions in Eugongyline skinks (Rosauer et al., 2015).

Cryptic speciation can likewise be thought of as a case where species-level genetic divergence is seen between taxa with within-species levels of morphological disparity (Struck et al., 2018). Lineages may be morphologically undiagnosable for several reasons, including long-term morphological stasis, recent divergence, and convergence, but only the first of these leads to cryptic speciation as defined in this framework (Chenuil et al., 2019; Fiser et al., 2018; Struck et al., 2018). Practically, this means that cryptic species pairs should show no relationship between genetic divergence and morphological disparity, as was observed in a cryptically evolving clade of frogs in southern India (Ramesh et al., 2020).

The purple cluster shows a positive correlation between morphological disparity and genetic divergence. This is more consistent with the predictions of gradual speciation (i.e., genetic and morphological changes accumulating in proportion to each other) than cryptic speciation, for which we would expect both low mean morphological disparity and no significant relationship between morphological disparity and genetic divergence. The morphologically undiagnosable pairs included in our analysis had significantly lower genetic divergence than the morphospecies pairs and did not show any pattern of low morphological divergence relative to genetic divergence. For this reason, these pairs are unlikely to represent "cryptic species" (i.e., species generated by the process of cryptic speciation) but are instead examples of recent divergence (Fiser et al., 2018). The two outlier pairs in the teal cluster with very low rates of morphological divergence may be examples of cryptic speciation, but no definitive pattern can be established from such a small number of data points.

It has been proposed that, for well-studied clades where α-taxonomy is reasonably complete, the level of morphological differentiation seen between described species should be a good guide for what is typical for species-level divergence (Chenuil et al., 2019; Struck et al., 2018), and that this standard could be used to designate species pairs as having more or less phenotypic disparity than expected for their level of genetic divergence (Struck & Cerca, 2019). However, for the species pairs in this data set, many morphospecies pairs are distinguished by characters which are unlikely to have any adaptive significance, such as subtle differences in scalation (e.g., Greer, 1991; Horner, 2007). There is no difference in the levels of morphological disparity shown by taxonomically recognized pairs and morphologically undiagnosable pairs in this data set, showing that phenotypic recognition of taxa is not necessarily correlated with eco-morphological disparity. While traits such as color and patterning are likely to be under selection (Olsson et al., 2013), and aspects of scalation have been correlated with ecological variables (Calsbeek et al., 2006), many scale characters shown to reliably track species boundaries in reptiles are likely to be evolving under neutral processes (Martinez-Castro et al., 2021). It is possible that the subtle, nonadaptive characters which are often used to delimit the species in this data set may have become fixed in diverging lineages through neutral processes and may therefore be a kind of proxy for neutral genetic divergence. If this is the case, then simply being a "morphospecies" is unlikely to provide insight into the relative importance of divergent adaptation compared to drift or stabilizing selection in the speciation process. Some recent studies have noted that minor phenotypic differences between otherwise highly similar taxa can facilitate taxonomic recognition but do not negate general patterns of eco-morphological stasis arising from the cryptic speciation process (Korshunova et al., 2019; Shin & Allmon, 2023). Morphometric traits, such as the ones used to estimate morphological disparity in this study, may be informative of an organism's ecology but poor diagnostic tools as they often form a cline within and between taxa along abiotic (e.g., latitudinal) gradients (Archie, 1985; Forsman & Shine, 1995; Laiolo & Rolando, 2001; Padial et al., 2010). Several of our morphologically undiagnosable pairs are sampled across such gradients which may explain their high morphological disparity estimates. We suggest that, in general, species need not be "truly cryptic" (i.e., a complete absence of distinguishing phenotypic traits) to be evolving under the cryptic speciation process as defined here.

We have demonstrated how the framework of Struck et al. (2018) can be applied to an empirical system to identify heterogeneity in divergence patterns across a radiation. Instead of pairs conforming to a single predictable relationship between morphological and molecular divergence, we show that pairs of named species and within-species pairs distribute in clusters that are either consistent with gradual acquisition of morphological and molecular divergence, or with a relatively more rapid rate of morphological change. Post hoc comparison of ecological disparity between these clusters shows that the more rapid rate of morphological divergence may be associated with topographic variables. In spite of the prior recognition of cryptic diversity within this clade, we did not find evidence for long-term morphological stasis leading to cryptic speciation. Our study highlights the value of comparative methods in characterizing divergence patterns across a clade to provide context to individual population histories (Johannesson et al., 2024).

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

Morphometric data are provided in the supplementary materials. All other data used are publicly available.

Author contributions

R. Schembri collected and wrangled the data and performed all the analyses. X. Hua devised the statistical analysis framework. C. Moritz provided expert advice on the study system. All authors contributed to conceptualization, broad study design, and interpretation of results. R. Schembri wrote the manuscript with input from all other authors.

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